RECIPROCAL TRANSLOCATION IN RICE

(A preliminary note)

by

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Structural change of the chromosomes seems to be little known in the rice plant, though it has been discovered early by Ramiah et al (1935). The writers investigated several semi-sterile strains induced by X-ray irradiation, and recognized their sterility was due to "reciprocal translocations". Some genetical and cytological observations of those strains will be reported in this paper.

Two varieties, Taichung no. 65 (a representative Horai or Japanese variety in Formosa) and Pei-ku-fua-lo (a native variety of first-crop-nature), were used. Germinating seeds were X-rayed by one of the writers, Chang, in the Agricultural College of National Taiwan University, on Feb. 14, 1948, and field tests were made in the Taiwan Agricultural Research Institnte. Dose of X-ray: 4 m. a., 80 k. v., 30 cm, 80 minutes. A number of semi-sterile plants, different in fertility even within a plant with the ear, were obtained from the X-rayed seeds. In the second generation, there were found several strains which gave fertile plants and semi-sterile plants (50–30% in fertility) in approximately 1:1 ratio. In the third generation and afterwards, the fertile plants were found to breed true, but the semi-sterile plants continued segreation in the same manner as in the second generation. Such a behavior of sterility seems to be of the same type as found by Ishikawa (1927) and other workers (2, etc).

Four strains of this type, taken arbitrarily from those, were observed in the Taiwan Provincial College of Agriculture by Oka and Hong. From each of these four strains, seed of one sterile plant was taken as the materials. Two of them, named XA-1 and XA-2, are the fourth generation seed of Taichung no. 65, and the other two, named XB-1 and XB-2, are the third generation seed of Pei-ku-fua-lo. All of the plants obtained from these seeds showed normal growth and were in appearance same to ordinal Taichung no. 65 or Pei-ku-fua-lo. Variations of the percentage of fertile grain in these strains are given in Table 1. Three strains, XA-2, XB-1 and XB-2, showed clearcut segeregation of fertile and semi-sterile plants, but XA-1 showed a seemingly continuous variation of fertility.

Secondly, several plants of each strain were back-crossed to original Taichung no. 65 or Pei-ku-fua-lo, using the former as the pollen parent. Fertility of paternal plants and the variation of fertility among the plants produced from the back-crosses are given in Table 2. In XA-1, the back-cross produced no sterile plant. In other three strains, however, the following facts were found as a general rule: Original variety x fertile plants produced either fertile or sterile plants and the segregation of fertile and sterile plants was never seen within the same cross. In contrast, ori-

ginal variety x semi-sterile plants produced both fertile and semi-sterile plants in the same manner as the selfing of semisterile plants.

Table 1. Variation of the percentage of fertile grain.

Strains	% of fertile grain								Total num. of plants
	90	80	70	60	50	40	30	20	
XA-1	3	4	9	10	12	3			41
XA-2	5	10 (19)	4		1	9 (20)	10		39
XB-1	7	1 (8)		14	2 (16)			1 ?	25
XB-2	2	9 (14)	3			2	4 (8)	2	22

Table 2. Segregation of fertile and semi-sterile plants in the hybrid between original variety and several plants of the used strains.

Crosses	Fertility of paternal plants (%)	Fertility of hybrid plants (%)									Total num. of plants
		90	80	70	60	50	40	30	20	10	
AxXA-1-1	57	3									3
" 2	87	2									2
" 3	54	4									4
" 4	52	5									5
" 5	75	3									3
" 6	62	1	2								3
AxXA-2-1	93	2									2
" 3	85						2				2
" 4	35	1					1				2
BxXB-1-1	59	1	4			3	4				12
" 3	54		1			2	1	1			5
" 4	88					3	2				5
" 5	55	1	7	2		3	5				18
" 6	55		1			1	1	1			4※
" 8	85					3	1				4
" 10	92					3	2				5
BxXB-2-1	82									4	4
" 2	24		1	1					1		3
" 3	79		3	8							11
" 4	28		1							1	2
" 5	29			1					1	1	3
" 6	80		3	7							10
" 7	23	2	1	1	1						5
" 8	85								1	4	5
" 9	81									4	4
" 10	27			6						4	10

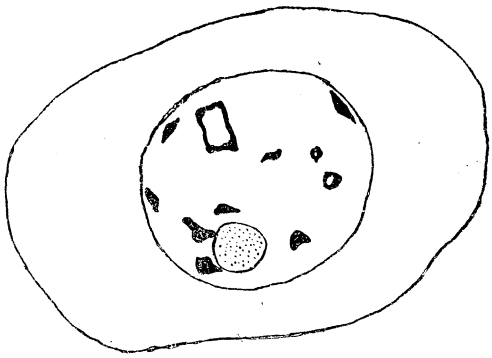
※Two plants were dwarf type. A: Taichung. no. 65
B: Pei-ku-fua-10

Such a behavior of sterility seems to suggest that the sterility is caused by a segmental interchange: Assuming that from two certain chromosomes which had been in structure 1-2 and 3-4 originally, a reciprocal translocation, 1-3 and 2-4, was induced by X-ray radiation, and the semi-sterile plants were of such a structure as $\frac{1\text{-}2,\ 3\text{-}4}{1\text{-}3,\ 2\text{-}4}$, the above mentioned phenomena will be explained without difficulty.

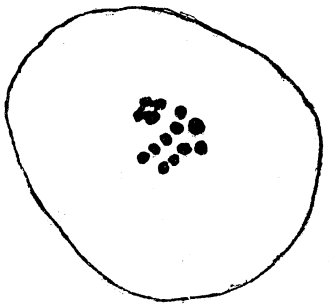
If it was really the case, a "ring of four" should be found in the meiosis of sterile plants. In order to see whether a ring quadrivalent chromosome would be found or not, pollen mother cells of several semi-sterile plants were observed. Fixative: Bouin solution, staining: iron haematoxylin.

Table 3 gives the observed number of various pairing types. There was found one quadrivalent chromosome in 1/5-2/5 of pollen mother cells, excepting XB-2. Particularly, in XA-2, eight cases of typical ring of four were found in addtion to 25 cases of chain shaped and 21 cases of quadrivalent of other shapes. In XA-1 and XB-1, quadrivalents of various other shapes were found (Fig. 1)

Fig. 1 Ring of four in pollen mother cells of XA-2 (x ca.2,000).



(Diakinesis)



(Metaphase I)

These differences in the frequency and shape of quadrivalent chromosomes may be due to the difference in chiasma frequency and fluctuation of the number and position of chiasmata. Assuming that chiasma frequency is proportional to chromosome length, the length of translocated segments may be estimated by the following calculation: Let us denote by x and y the chiasma frequencies in translocated segments, and by u and v those between the point of interchange

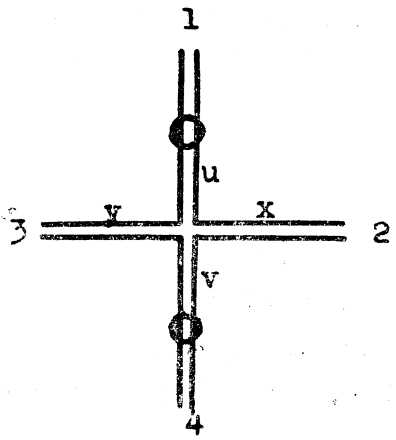


Table 3. Types of chromosome pairing in semi-sterile plants.

Strains & no. of plants	Stage	12Ⅱ	11Ⅱ+2Ⅰ	10Ⅱ+4Ⅰ	1Ⅳ+10Ⅱ	1Ⅳ+9Ⅱ+2Ⅰ	Others	Num. of cells observed
XA-1-1	Diaki.	9	1		2			12
XA-1-3	Diaki.	21	1		17	1		40
„	Meta-Ⅰ	18			16		1*	35
XA-1 in total		48	2		35	1	1	87
XA-2-4	Diaki.	17	2	1	22	8	1**	51
XA-2-7	Diaki.	1			3	1		5
„	Metat Ⅰ	8			5			13
XA-2-8	Diaki.	6	4	1	14	6		31
„	Meta-Ⅰ	21			10			31
XA-2 in total		53	6	2	54	15	1	131
XB-1-1	Diaki.	15			4			19
„	Meta-Ⅰ	8			3			11
XB-1-2	Diaki.	22	2		4	2		30
„	Meta-Ⅰ	10	1		3			14
XB-1-6	Diaki.			2	2	2	4***	10
XB-2 in total		55	3	2	16	4	4	84
XB-2-2	Diaki.	4	1					5
„	Meta-Ⅰ	12						12
XB-2-5	Meta-Ⅰ	9						9
XB-2 in total		25	1					26

* 2Ⅳ+8Ⅱ, ** 1Ⅲ+10Ⅱ+1Ⅰ, *** 1Ⅳ+8Ⅱ+4Ⅰ, 1Ⅳ+7Ⅱ+6Ⅰ, 8Ⅱ+8Ⅰ

and kinetochore (the diagram given above), then the frequencies of quadrivalents of different shapes will be related in the following way:

Freq. in XA-2

Quadrivalents in total=x+y−xy	55/87
Ring shaped=xy (1−u)(1−v)	8/87
Chain shaped=(x+y−2xy)(1−u)(1−v)	25/87
Other shapes=(x+y−xy)(u+v−uv)	21/87

Solving these equations, x=0.43, y=0.36, (or x=0.36, y=0.43) will be obtained for the given strain, XA-2. It is impossible to find the values of u and v, but the average of u and v will be found to be 0.22 by assuming u=v. According to these calculations, the length of translocated segments in this strain seems to be approximately two thirds of an arm of chromosome.

In XB-1, quadrivalents were found in 23 out of 84 cells observed, but typical ring and chain were not found. Translocated segments seem, therefore, to be considerably shorter than those of XA-2. One plant of this strain, XB-1-6, showed irregular behaviors of the chromosomes, and produced few dwarf plants from the cross with the original Pei-ku-fua-lo.

XB-2 showed no quadrivalent, but considering from the inheritance of sterility as shown in Table 2, this strain may have a reciprocal translocation. Possibly translocated segments may be very short and invisible under the microscope.

XA-1 may have some structural change, as a quadrivalent chromomsome has been found in a part of pollen mother cells. But the inheritance of sterility has been, as given in Table 2, different from what is expected as a translocation heterozygote. It may be possible to suppose that the cause of sterility in this strain is inherited only through female gametes. Further studies are necessary for proving this supposition.

Few cells containing two univalents were found in all of these four strains. The occurrence of univalents seemed to have nothing to do with the formation of quadrivalents. Further, minute fragments, one to six in number, were found in some diakinetic nuclei. The number differed even within the same anther, and they were not found at metaphase probably because of the elimination from the equatorial plate.

It will be concluded, according to these observations, that in at least three of the four strains examined, the sterility is attributable to a reciprocal translocation. One to one segregation of semi-strile plants in rice has been reported by a number of workers (3, etc). Some part of them may be due to a reciprocal translocation in the same manner as in the present materials, though it has not been demostrated. It was reported recently in Japan that a greater part of sterile rice plants found after the explosion of Atomic Bomb at Hiroshima as well as at Nagasaki showed quadrivalent chromosomes in the meiosis, (4, 5). Considering these facts, translocation seems to occur relatively frequently by artificial irradiation in the rice plant. As it is a useful materials for linkage analysis and other genetical studies (7), the writers are now on the way to prepare more strains such as found in the present work.

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稻種X線處理後發生之染色體"相互轉位"

—— 預　　報 ——

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就臺中 65 號及白殼花螺二品種之萌芽種子，用X線以 4m.a, 80 K. V. 及 30cm. 之距離，照射 80 分鐘。在處理後第二代發現甚多系統，約依 1 與 I 之比，分離爲稔實稻與半不稔稻在後代中稔實稻固定，半不稔稻則繼續作 1 比 1 之分離。半不稔稻之結實率約自 20 至 50%。茲就白殼花螺任取第三代二系統 (XB-1,XB-2) 及臺中 65 號任取第四代二系統 (XA-1,XA-2)，作遺傳及細胞方面之考察。

XA-2,XB-1,XB-2 呈明顯之稔實稻 1 比半不稔稻 1之分離，但 XA-1 則呈連續性結實率之分離。以上列系統作父本與原品種作回交之結果，就 XA-1 後代中無不稔稻發生，但在其餘三系統以稔實稻與原品種回交，則發生全部稔實稻或全部不稔稻，以半不稔稻與原品種回交，則同時發生稔實稻與半不稔稻，如半不稔稻之自交後代然。此項遺傳行爲顯示有"相互轉位" 現象之存在，半不稔稻似係由於射線之影響，所造成之"轉位異型體" (Translocation heterozygote)。

再就各系統作細胞學觀察，發現除 XB-2 外，約 $\frac{1}{5}$ 至 $\frac{2}{5}$ 之花粉母細胞有一個四價染色體，其發生頻度及形狀頗多變異，似由于交叉 (Chiasma) 頻度及其數目及位置之不同，設交叉頻度與染色體長度成正比，則可計算轉位部分之長度。

在 XA-2 中，除鏈形及其他形狀之四價染色體外，發現典型之環形四價染色體 (Ring of four) 最多，其轉位部分之長度經計算約當一染色體臂之 $\frac{2}{3}$。在 XB-1, 雖有若干四價染色體，而未發現典型之環形或鏈形者，可見其轉位部分遠較爲短。 XB-1, 全無四價染色體發現，但就其遺傳行爲觀之，當亦發生"相互轉位," 或其轉位部分過短，而不可見。在 XA-1, 亦有四價染色體出現，但其遺傳行爲不同於前三系統，或其不稔性係僅由雌配子遺傳者。

綜合細胞及遺傳學的證據，至少 XA-2, XB-1, XB-2 三系統之不稔性可歸因於 "相互轉位"，此等材料對於連鎖現象之分析及其他遺傳學研究，甚有價值。